Selbyana 25(1): 118–125. 2004.

VERTICAL DISTRIBUTION OF EPIPHYTIC AND HEMIEPIPHYTIC ARACEAE IN A TROPICAL RAIN FOREST IN CHOCÓ, COLOMBIA

JORGE JÁCOME,* GLORIA GALEANO, MARISOL AMAYA, AND MARCELA MORA

Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia.
E-mail: jjacome@gmx.net

ABSTRACT. To determine if different habitat preferences and habitat segregations exist among epiphytic and hemiepiphytic Araceae, we recorded the heights above the ground among adult Araceae at Cabo Corrientes, Colombia. A differential vertical distribution was found among the aroid genera, the subgenera of *Anthurium* and *Philodendron,* and the species when analyzed independently. Distribution along the vertical gradient appears to be related to growth forms and morpho-physiological adaptations to the canopy environment, such as litter-trap growth, thick cuticles, and ramification type. Our results indicate that despite the importance that stochastic processes could have in maintaining species-rich assemblages in tropical forest, habitat differentiation also is detectable and appears to be playing a role in determining the high species richness of Araceae in the forest of the Pacific coast of Colombia.

Key words: diversity maintenance, epiphytes, growth forms, hemiepiphytes, leaf morphology, habitat differentiation

INTRODUCTION

The coexistence of large numbers of closely related plant species in limited areas has attracted the attention of many ecologists and set one of the guidelines of research in ecology: the origin and maintenance of high local species diversity (Richards 1964, Schluter & Ricklefs 1993, De Kroon & Olff 1995, Gaston & Williams 1996). High local species richness may be a consequence of niche segregation among species (Tilman 1982, Schoener 1989) or environmental constraints, such as disturbance, herbivory, or pathogens. Such population-limiting factors may prevent competition as a consequence of space or resource saturation (Benzing 1978, Price 1984, Colwell & Lawton 1992).

High species richness in limited areas frequently has been observed in tropical forests, especially among non-woody plants (Dodson & Gentry 1978, Gentry & Dodson 1987, Hammel 1994, Foster & Hubbell 1994, Balslev et al. 1998). Species richness occurs particularly in taxa with epiphytic or hemiepiphytic growth habits, such as Orchidaceae, Araceae, and Pteridophytes (Galeano et al. 1998a, Nieder et al. 1999).

In the tropical rain forest along the Pacific coast of the department of Chocó, Colombia, the richest species taxon is the Araceae. In a 0.9-ha sample, Araceae accounted for 10% (100 species) of all the vascular plant species (Galeano et al. 1998a). This high species richness was represented by epiphytic and hemiepiphytic species mainly of the genera *Anthurium* and *Philodendron.*

Among the Araceae, different habitat preferences have been described that may relate to the autoecology of the species. In the forest, these preferences may determine the position along the vertical gradient of species with epiphytic and hemiepiphytic growth habits. With the exception of a study by Nieder et al. (2000), the vertical distribution patterns of Araceae have been described based on few species (Kernan & Fowler 1995, Mantovani 1999), rather than on all species occurring at a study site. The patterns described by Neider et al. (2000) illustrated differences in the vertical distribution among the Araceae genera, but whether these differential patterns also are present among infrageneric groups and species in a genus remains unknown.

In this research, we studied the vertical distribution patterns of hemiepiphytic and epiphytic Araceae species in an especially aroid-rich area along the Pacific coast of Colombia. Our purpose was to establish if the coexistence of large numbers of aroid species in this area could be facilitated by differential vertical distribution (habitat segregation) among species and to determine if different habitat preferences are evident among infrageneric groups and species.

METHODS

Study Area

The study was conducted from January to April 1999 in a tropical wet forest at "El Amar-

*Corresponding author: Current address, Albrecht-von-Haller-Insitut für Pflanzenwissenschaften. Abteilung Systematische Botanik, Untere Karspüle 2, 37073 Göttingen, Germany.

gal" Biological Station (5°34′N, 77°31′W), in Cabo Corrientes peninsula, on the Pacific coast of the Department of Chocó, Colombia. Mean annual precipitation is 7245 mm, and mean annual temperature is 25°C (IDEAM and Fundación Inguedé, unpubl. data). The relative humidity usually remains above 90%. This region has a hilly-undulated topography, not higher than 200 m and with slopes of 10–50°. The area is covered mainly by non-disturbed tropical wet forest, according to the Holdridge classification system (IGAC 1977) with selective logging of some tree species (Galeano et al. 1998b). Details regarding vegetation structure and composition of the area can be found in Galeano et al. (1998a, 1998b) and Galeano (2001).

Data Collection

In an area of 1 km^2, along five 1-km-long transects perpendicular to the coastline, 25 plots of 400m^2 were situated every 250 m, providing a total sampling area of 1 ha. In these plots, all adult epiphytic and hemiepiphytic Araceae were recorded, vouchered, and measured for height above ground. For plants with hemiepiphytic or epiphytic-scandent growth habit, height was measured at the highest point reached by the plant. Height of individual plants was established through telescopic clipper pole tubes of 1.5 m, divided in 4 sections of 32.5 cm. Plants that presented no connections with another were considered as independent individuals (Leimbeck & Balslev 2001). Differentiation of adult and juvenile plants was made by observing the presence of reproductive structures or mature morphological features, such as shape and size of leaves that vary from juvenile to adult stages (Mayo et al. 1997).

To survey the upper stories of the forests, single rope climbing methods were used (Ter Steege & Cornelissen 1988). Vouchers were deposited at the Universidad Nacional de Colombia Herbarium (COL) and the Missouri Botanical Garden Herbarium (MO). Determinations were carried out by T. Croat and M. Grayum (MO) and M. Mora and J. Jácome (COL).

Data Analysis

Non-parametric statistics were applied, because the variable height was not normally distributed (Fowler et al. 1998). To determine if a vertical differential distribution existed among genera and subgeneric groups and species in each genus of Araceae, we conducted Kruskall-Wallis and U-Mann-Whitney tests. To avoid biases caused by inaccurate distributions, we excluded from analysis species with less than ten recorded individuals.

Results

For the 25 plots sampled, 2957 adult individuals of 52 species and 7 genera of epiphytic Araceae were recorded. In the distribution analyses, 2919 individuals of 41 species and 6 genera were considered (Appendix).

The Araceae genera studied had different vertical distribution patterns in the forest (Kruskal-Wallis-Test: H (5, N = 2955) = 334.49 $P <$ 0.001). All genera were present at different heights, with exception of *Philodendron* and *Monstera,* which presented similar distribution patterns (Figure 1). Most of the Araceae genera were distributed at 0–10 m in the forest, with exception of the genera *Stenospermation* and *Anthurium,* which surpassed this height and were found mainly at 10–20 m in height. Wide ranges of vertical distribution, however, were observed especially for the genera *Anthurium* and *Philodendron.*

The taxonomic sections of *Anthurium* had different vertical distribution patterns (Kruskal-Wallis-Test: H (5, N = 839) = 110.68 $P <$ 0.001). Species of sections *Leptanthurim* and *Porphyrochitonium* were located principally above 10 m, whereas species of the sections *Belolonchium, Calomystrium, Digitinervium,* and *Dactylophyllum* were found to grow at 0–10 m in height (Figure 2).

A difference occurred in the vertical distribution patterns of the subgenera of *Philodendron* (U = 176191, z = −13.9, P <0.01). *Philodendron* subgen. *Pteromischum* was found restricted to lower heights, whereas subgen. *Philodendron* was distributed along the entire vertical gradient (Figure 3).

We detected differences of vertical distribution among species of *Anthurium, Philodendron, Monstera,* and *Stenospermation* (Table 1).

Discussion

The Araceae in Pacific coast forests grow preferentially in the first 10 m of the vertical gradient (Figure 1), as previously reported for other tropical rain forests (Ter Steege & Cornelissen 1989). The preference or partial restriction of the Araceae to the understory level in the forest may be a consequence of the lack of major adaptations to the xeric environmental constraints of the epiphytic habitats (Benzing 1990). Genera with epiphytic species, such as *Stenospermation* and *Anthurium,* however, were observed at higher levels, indicating a morphological or physiological heterogeneity among the

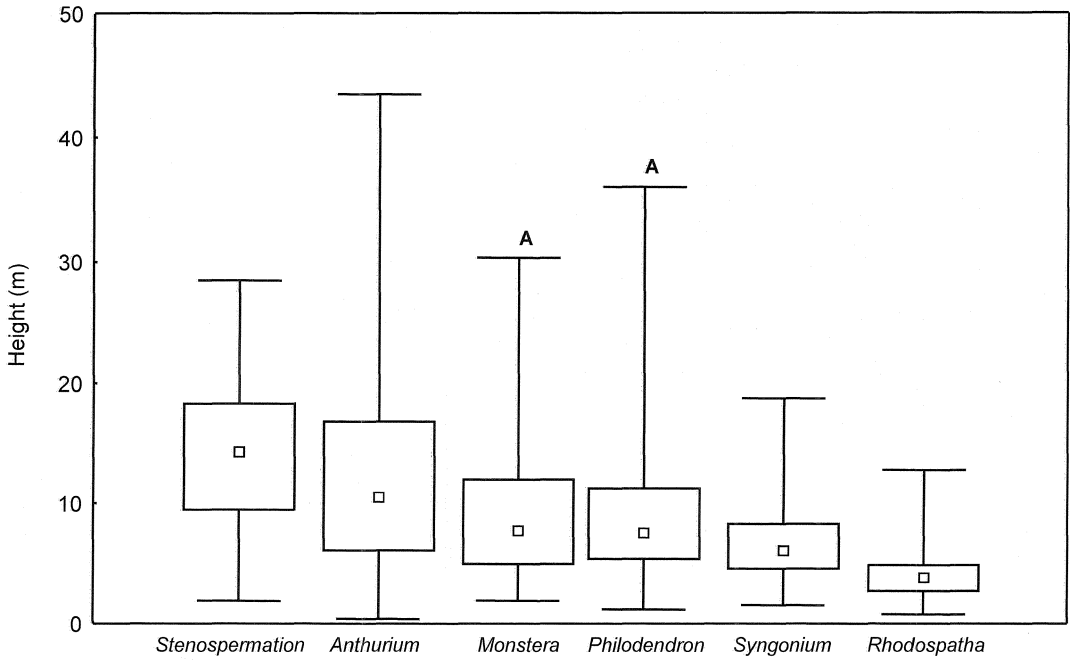

FIGURE 1. Median, quartiles, and maximum and minimal height of the Araceae genera in a tropical forest in Cabo Corrientes. Genera with the same letter indicate no significant differences in the height distribution between them.

aroids. This heterogeneity previously was observed by Mantovani (1999), through analysis of leaf morpho-physiological features. He found that Araceae, which adapted to the xeric canopy condition, had succulent leaves and thick cuticles. In our study area, these features may allow the establishment of some species and subgeneric groups in the canopy level, determining an adaptation gradient among the Araceae. In *Anthurium,* the species of sections *Porphyrochitonium* and *Leptanthurium* were distributed higher than species of other sections (FIGURE 2). In particular, *A. paludosum* (sect. *Porphyrochitonium)* and *A. friedrichsthalii* (sect. *Leptanthurium*) differed morphologically from the other species, by having succulent leaves protected by thick cuticles. The other *Porphyrochitonium* species were characterized by short and thick stems, with leaves around the stem in a rosette. These morphological features of *Porphyrochitonium* species, which give them the common name of birds' nests, increase the interception of litterfall and rainwater (Sheridan 1994). In this way, the species could be facilitating their presence at higher levels, operating in a way analogous to tank-type bromeliads (Benzing 1990). The differential distribution patterns among taxa, such as the one described for the sections of *Anthurium,* previously have been described for Bromeliaceae (Benzing 1990), with xerophytic, mesophytic, and hygrophytic species.

In *Philodendron,* we observed a differentiation in the habitat preferences along the vertical gradient among subgenera, which may be related to morphological features of the groups (FIGURE 3). Subgenus *Pteromischum,* which shows a preference for understory environments, is characterized morphologically by a reduced foliar area, membranaceous leaf consistency and by its sympodial growth with indeterminate number of leaves in the lateral branches (Grayum 1996, Croat 1997). This growth habit, which implies greater production of lateral shoots and leaves, together with reduction in the foliar area and membranaceous consistency of the leaf may be operating as a successful adaptative mechanism to the low irradiation and high humidity conditions of the understory level. In contrast, species of the subgenus *Philodendron,* mainly distributed above species of *Pteromischum,* have physiognomically monopodial growth, in which the apical meristem produces usually only one leaf and one inflorescence, the vegetative growth continues in a subjacent lateral meristem, and branching is present only when the apical meristem does not produce flowers (Croat 1997). The physiognomically monopodial growth of subgen. *Philodendron* may limit the production

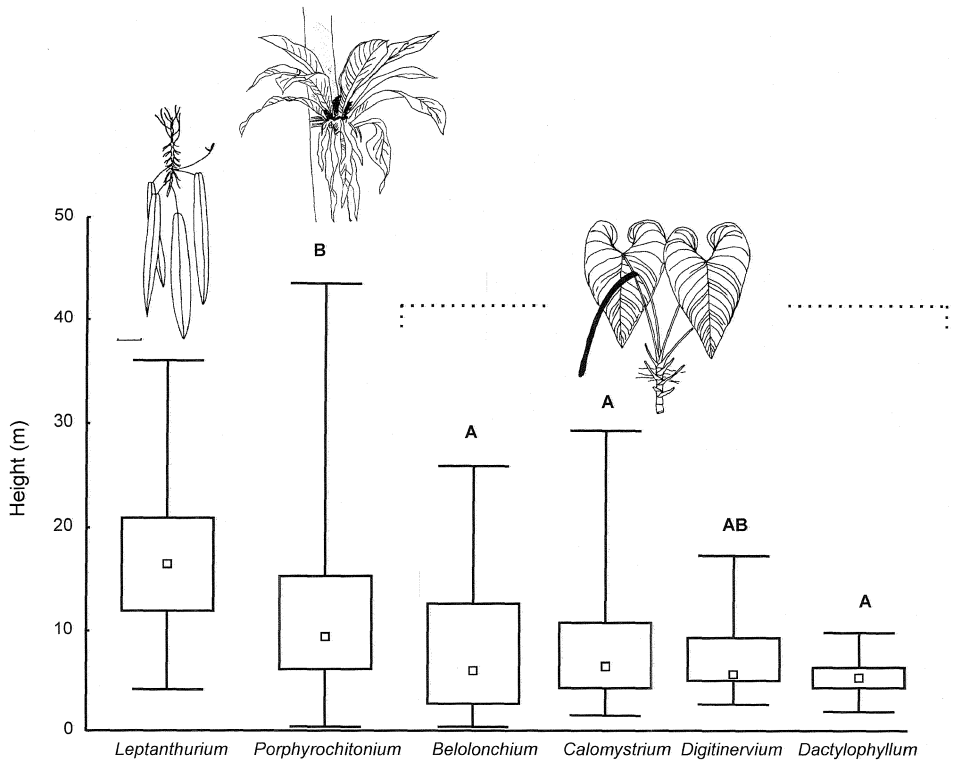

FIGURE 2. Median, quartiles, and maximum and minimal height and growth form of *Anthurium* sections in a tropical forest in Cabo Corrientes. Sections with the same letter indicate no significant differences in the height distribution between them.

of large numbers of leaves, as in subgen. *Pteromischum,* which may be in response to an irradiation deficit in the understory and a preference for middle heights. The increased leaf area and prevalence of cordate leaf forms in subgen. *Philodendron* may be operating as an adaptative mechanism related to the limited production of leaves and the light deficit in the understory.

Despite an overlap in the vertical distribution of some species, differential distribution patterns among the Araceae species were observed, suggesting a niche separation among them (APPENDIX, TABLE 1). Niche separation patterns have been reported to represent environmental heterogeneity (Lieberman et al. 1985, Hubbell & Foster 1986) or to be a consequence of competition among related species (Tilman 1982). In this way, the spatial separation among Araceae may indicate not only different habitat preferences but also competitive interactions. No empirical evidence was found to indicate that spatial saturation may be driving competition in the Araceae community of Cabo Corrientes, and no findings were recorded of possible interspecific competitive interactions at reproductive level, such as pollen transfer interference. Studies, nonetheless, have established that neotropical aroids possess highly specialized pollination mechanisms (Croat 1997), which may make the maintenance of highly diverse and dense "species-packing" Araceae communities possible (Grayum 1996, Schwerdfeger et al. 2002). In this way, a differential vertical distribution may indicate that reproductive competitive interactions previously occurred and could be operating as a mechanism to reduce pollen interference, because pollinators are documented to have preferences to particular habitats or stories in the forest (Seres & Ramírez 1995, Ramírez 1993). Within the genera *Stenospermation, Monstera, Syngonium,* and *Rhodospatha,* such a habitat segregation process could explain the finely tuned vertical differentiation among the species, for which no evident morphophysiological differences were observed.

In a tropical forest with fewer aroid epiphytic species in Surumoni, Venezuela, Nieder et al. (2000) found differences in the vertical distribution pattern between *Anthurium* and *Philodendron,* which seem to be consistent with growth

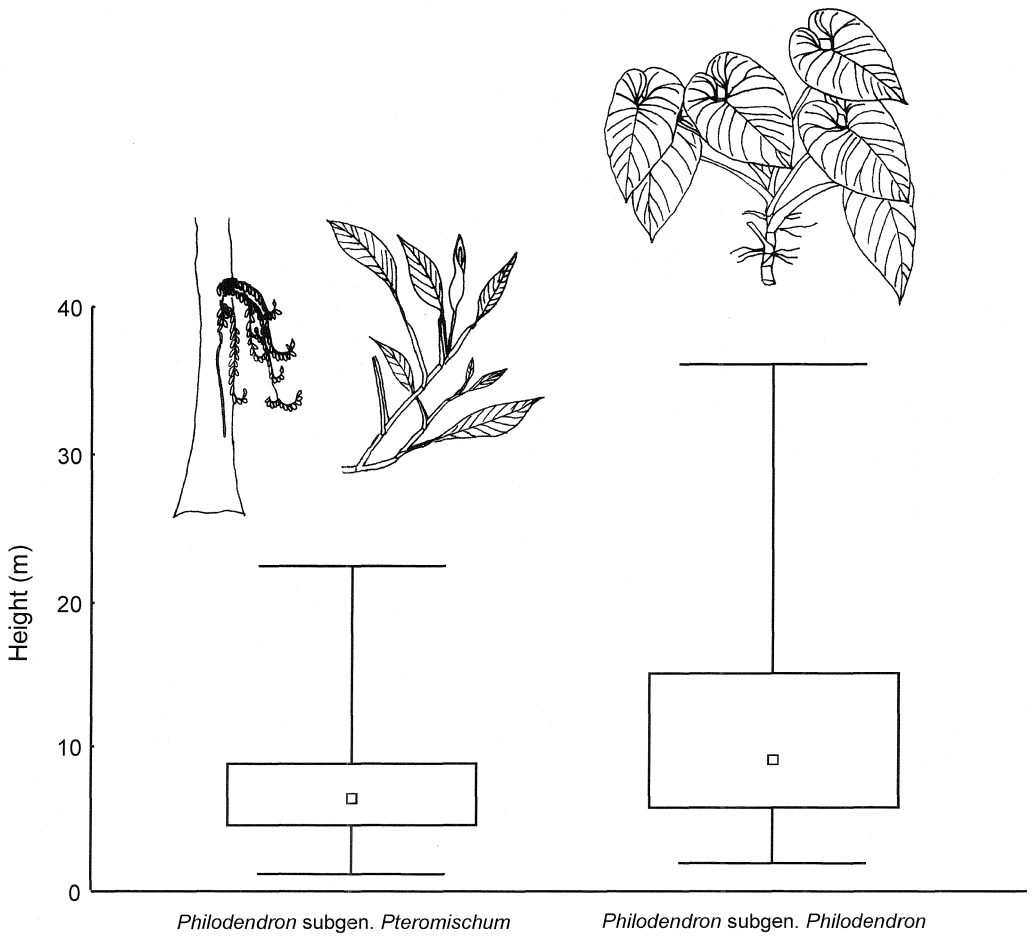

FIGURE 3. Median, quartiles, maximum and minimal height, and growth form of *Philodendron* subgenera in a tropical forest in Cabo Corrientes.

habit differences (epiphytic and hemiepiphytic) of these genera in the area. In our research, the vertical differentiation patterns were more finely tuned, involving more genera, and were observed within species of a genus and among subgeneric or sectional groups. This clear vertical separation pattern could be a consequence of the greater number of aroid species in the Chocó area, involving more defined habitat differentiation, and possibly competitive interactions. Interspecific competition could be more important in some epiphytic plant communities than in others. Such a situation has been documented for aroid communities in flood plain and terra firme forests in Amazonian Ecuador, where the density of phorophytes becomes a limiting factor (Leimbeck & Balslev 2001). Thus, even in the same plant family, changes in environmental conditions may subject communities to different constraints. The search for a single mechanism that determines the coexistence of species in tropical forest may be flawed and unhelpful.

According to our results, the Araceae show different and well-defined habitat preferences

TABLE 1. Summary of Kruskall-Wallis ANOVA (Analysis of Variance) in vertical distribution of species within the Araceae genera in the study area. df = degrees of freedom. *N* = number of individuals. H = statistical value of the test. *P*-value = probability.

Genera	df	*N*	H	*P*-value
Anthurium	11	839	332.8	0.01
Monstera	3	107	59.71	0.001
Philodendron	16	1563	570.02	0.01
Rhodospatha	2	90	7.89	0.019
Stenospermation	2	259	92.37	0.0001
Syngonium	1	61	2.83	0.09

APPENDIX. List of Araceae species reported from Cabo Corrientes, with number of individuals (*N*) and mean, standard deviation, minimum, maximum, median, low quartile, and upper quartile of the height along the vertical gradient.

Species	*N*	Mean	SD	Min	Max	Median	Lower quartile	Upper quartile
Anthurium acutangulum	71	7.6	4.1	1.1	18.4	6.4	4.5	10.5
A. brownii	22	14.3	5.4	5.3	25.9	14.3	10.5	18.0
A. cucullispatshum	27	12.0	5.6	1.5	23.6	12.3	7.5	15.8
A. emminens	10	5.4	2.4	1.9	9.8	5.3	4.1	6.4
A. friedrichsthalii	248	16.6	6.0	4.1	36.0	16.5	11.8	21.0
A. hacumense	171	9.8	5.5	0.4	28.5	9.0	5.3	12.8
A. paludosum	64	22.5	6.6	10.5	43.5	21.7	18.1	27.3
A. panamense	28	3.4	2.6	0.4	11.3	2.8	1.7	4.3
A. ravenii	58	10.1	5.9	1.5	29.3	8.6	6.4	12.0
A. subsignatum	62	4.5	2.1	1.9	12.0	3.9	3.0	5.3
A. indet sp. 1	65	9.3	5.0	1.5	23.3	8.3	5.6	12.0
A. indet sp. 2	13	7.2	4.1	2.6	17.3	5.6	4.9	9.4
Monstera minima	25	4.6	2.2	1.9	9.8	4.1	3.0	4.9
M. pinnatipartita	28	7.8	2.7	4.1	13.1	7.3	5.6	10.5
M. pittieri	20	17.9	5.2	12.8	30.4	17.6	13.6	18.5
M. spruceanum	34	8.0	3.5	2.3	13.5	7.7	5.6	10.5
Philodendron alliodorum	430	6.7	2.9	1.1	22.5	6.4	4.5	9.0
P. bakeri	70	19.9	6.1	3.0	30.4	20.7	16.5	24.0
P. croatii	28	7.4	4.8	2.6	18.8	5.3	3.8	11.1
P. ensifolium	14	7.3	2.9	2.6	10.9	6.6	4.9	10.5
P. fragrantissimum	208	5.8	1.7	1.9	12.0	5.6	4.5	6.7
P. hederaceum	154	21.0	7.1	1.9	36.0	21.0	15.7	26.3
P. heleniae	63	13.2	5.9	3.8	28.5	12.0	8.6	16.5
P. jodavisianum	79	6.8	2.1	2.6	13.5	6.7	5.6	7.5
P. ligulatum	37	10.3	3.3	3.0	15.8	10.1	8.2	12.0
P. opacum	17	3.9	2.4	1.5	10.5	3.0	2.2	5.2
P. platypetiolatum	34	8.8	3.6	3.0	16.5	8.4	6.0	10.8
P. pseudoauriculatum	105	8.4	4.3	1.9	22.5	7.5	5.2	10.5
P. rayanum	152	6.6	3.1	1.5	19.9	6.4	4.5	8.2
P. sagittifolium	88	10.5	3.9	3.0	19.9	10.5	7.5	13.5
P. sulcatum	27	8.1	3.9	1.9	15.8	6.7	5.6	11.6
P. sulcicaule	29	12.6	4.7	2.6	23.3	13.1	11.6	15.0
P. tripartitum	28	10.1	3.9	3.0	17.3	10.5	8.2	12.3
Rhodospatha monsalve	15	2.7	1.7	0.8	7.1	2.6	1.6	3.6
R. pellucida	23	4.4	1.9	1.5	9	4.1	2.6	5.7
R. wendlandii	52	4.3	2.6	1.1	12.8	3.8	2.3	5.3
Stenospermation angustifolium	42	18.6	4.6	7.9	27.0	18.9	16.5	21.0
S. multiovulatum	67	8.5	4.0	1.9	20.6	8.5	5.6	10.5
S. robustum	150	15.7	5.5	3.8	28.5	15.8	12.3	18.8
Syngonium llanoense	28	5.5	2.3	1.5	9.8	5.8	3.7	7.5
S. macrophyllum	33	7.6	4.3	3.0	18.8	6.0	4.5	9.0

along the vertical gradient, which seems to correspond in some cases to morpho-physiological features and growth forms of the species and subgeneric groups. Thus, although stochastic dynamics may play an important role in the maintenance of species richness in epiphytic environments (Nieder et al. 1999), habitat differentiation processes and possibly interspecific competition at reproductive level also may be operating.

ACKNOWLEDGMENTS

We thank the Fundación Inguedé, the Universidad Nacional de Colombia, Instituto de Ciencias Naturales, and the Herbario Nacional Colombiano (COL) for logistic and financial support during this research. Without the interest and help of K. Poveda, T. Croat, M. Grayum, and Arusí staff, this project would not have been possible. We thank Michael Kessler, Tom Croat, and two anonymous reviewers for the revision of the manuscript and their helpful comments.

LITERATURE CITED

Balslev, H., R. Valencia, G. Paz y Miño, H. Christensen and I. Nielsen. 1998. Species count of vascular plants in one hectare of humid lowland for-

est in Amazonian Ecuador. Pp. 585–594 *in* F. Dallmeier and J.A. Comiskey, eds. Forest Biodiversity in North, Central and South America, and the Caribbean. Unesco, Paris.

Benzing, D.H. 1978. Germination and early establishment of *Tillandsia circinnata* Schlecht. (Bromeliaceae) on some of its hosts and other supports in southern Florida. Selbyana 5: 95–106.

———. 1990. Vascular Epiphytes: General Biology and Related Biota. Cambridge University Press, New York.

Colwell, H.V. and J.H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. J. Animal Ecol. 61: 1–12.

Croat, T.B. 1997. A revision of *Philodendron* subgen. *Philodendron* (Araceae) for Mexico and Central America. Ann. Missouri Bot. Gard. 84: 311–704.

Croat, T.B. and R.D. Sheffer. 1983. The sectional groupings of *Anthurium* (Araceae). Aroideana 6: 85–123.

De Kroon, H. and H. Olff. 1995. On the use of the guilds concept in plant ecology. Folia Geobot. Phytotax. 30: 375–387.

Dodson, C.H. and A.H. Gentry. 1978. Flora of the Rio Palenque Science Center. Selbyana 4(1–6): 1–628.

Foster, R.B. and S.P. Hubbell. 1994. The floristic composition of Barro Colorado Island Forest. Pp. 85–98 *in* A.H. Gentry, ed. Four Neotropical Rain Forests. Yale University Press, New Haven.

Fowler, J., L. Cohen and P. Jarvis. 1998. Practical Statistics for Field Biology. John Wiley & Sons, England.

Galeano, G. 2001. Estructura, riqueza y composicion de plantas leñosas en el Golf de Tribugá, Chocó, Colombia. Caldasia 23(1): 213–236.

Galeano, G., S. Suárez and H. Baslev. 1998a. Vascular plant species count in a wet forest in Chocó area on the pacific coast of Colombia. Biodivers. & Conserv. 7: 1563–1575.

Galeano, G., J. Cediel and M. Pardo. 1998b. Structure and floristic composition of a one hectare plot of wet forest at Pacific coast of Chocó, Colombia. Pp. 551–568 *in* F. Dallmeier and J.A. Comiskey, eds. Forest Biodiversity in North, Central and South America, and the Caribbean. Unesco, Paris.

Gaston, K.J. and P.H. Williams. 1996. Spatial patterns in taxonomic diversity. Pp. 202–229 *in* K.J. Gaston, ed. Biodiversity: A Biology of Numbers and Difference. Blackwell Science, Oxford.

Gentry, A.H. and C.H. Dodson. 1987. Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19(2): 149–156.

Grayum, M.H. 1996. Revision of *Philodendron* subgenus *Pteromischum* (Araceae) for Pacific and Caribbean Tropical America. Monogr. Syst. Bot. Missouri Bot. Gard. 47: 1–233.

Hammel, B. 1994. The distribution of diversity among families, genera and habit types in the La Selva flora. Pp. 75–84 *in* A.H. Gentry, ed. Four Neotropical Rain Forests. Yale University Press, New Haven.

Hubbell, S.P. and R.B. Foster. 1986. Biology, chance and history and the structure of tropical rain forest tree communities. Pp. 314–325 *in* J. Diamond and T.J. Case, eds. Community Ecology. Harper and Row, New York.

IGAC (Instituto Geográfico "Agustín Codazzi"). 1977. Zonas de vida o formaciones vegetales de Colombia. Memoria explicativa sobre el mapa Ecológico. Bogotá.

Kernan, C. and N. Fowler. 1995. Differential substrate use by epiphytes in Corcovado National Park, Costa Rica: a source of guild structure. J. Ecol. 83: 65–73.

Leimbeck, R.M. and H. Balslev. 2001. Species richness and abundance of epiphytic Araceae on adjacent floodplain and upland in Amazonian Ecuador. Biodivers. & Conserv. 10: 1579–1593.

Lieberman, M., D. Lieberman, G.S. Hartshorn and R. Peralta. 1985. Small-scale altitudinal variation in low wet tropical forest vegetation. J. Ecol. 73: 505–516.

Mayo, S.J., J. Bogner and P.C. Boyce. 1997. The Genera of Araceae. Royal Botanical Gardens, Kew.

Mantovani, A. 1999. Leaf morpho-physiology and distribution of epiphytic aroids along a vertical gradient in a Brazilian rain forest. Selbyana 20(2): 241–249.

Nieder, J., S. Engwald and W. Barthlott. 1999. Patterns of neotropical epiphyte diversity. Selbyana 20(1): 66–75.

Nieder, J., S. Engwald, M. Klawun and W. Barthlott. 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane Plot) Southern Venezuela. Biotropica 32(3): 385–396.

Price, P.W. 1984. Communities of specialists: a vacant niche in ecological and evolutionary time. Pp. 510–523 *in* D.R. Strong, D. Simberloff, L.G. Abele and A.B. Thistle, eds. Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, New Jersey.

Ramírez, N. 1993. Estratificación de los sistemas de polinización en un arbustal de la Guayana venezolana. Rev. Biol. Trop. 41(3): 471–481.

Richards, P.W. 1964. The Tropical Rain Forest: An Ecological Study. University Press, Cambridge.

Schluter, J. and R.E. Ricklefs. 1993. Species Diversity: An Introduction to the Problem. Pp. 1–10 *in* R.E. Ricklefs and J. Schluter, eds. Species Diversity in Plant Communities. Chicago University Press, Chicago.

Schoener, T.W. 1989. The ecological niche. Pp. 79–113 *in* J.M. Cherrett, ed. Ecological Concepts: The Contribution of Ecology to Understanding of the Natural World. Blackwell Scientific, Oxford.

Schwerdtfeger, M., G. Gerlach and R. Kaiser. 2002. Anthecology in the neotropical genus *Anthurium* (Araceae): a preliminary report. Selbyana 23(2): 258–267.

Seres, A. and N. Ramírez. 1995. Biología floral y polinización de algunas monocotiledoneas de un bosque nublado venezolano. Ann. Missouri Bot. Gard. 82: 61–81.

Sheridan, R.P. 1994. Adaptative morphology of the tropical wet montane epiphyte *Anthurium hookeri.* Selbyana 15(2): 18–23.

Ter Steege, H. and J.H.C. Cornelissen. 1988. Collect-

ing and studying bryophytes in the canopy of standing rain forest trees. Pp. 285–290 *in* J.M. Glime, ed. Methods in Bryology: Proc. Bryol. Meth. Workshop, Mainz. Hattori Bot. Lab., Nichianan.

———. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest in Guyana. Biotropica 21: 331–339.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, New Jersey.